RESEARCH

Successional trends and processes on a glacial foreland in Southern Iceland studied by repeated species counts

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Abstract

Introduction: Primary succession on glacial forelands is increasingly relevant as rapid glacial retreat is exposing growing land areas to plant colonization. We investigated temporal trends, controls, and outcomes in floral succession on a subarctic glacial foreland. Specifically, we examined changes in community composition (mosses, low shrubs, forbs, trees, and graminoids) over long-term (decadal) and short-term (< 10 years) scales and attempted to identify the underlying processes responsible for the observed successional patterns.

Methods: The study area was the foreland of the Skaftafellsjökull, located in Vatnajökull National Park near the south coast of Iceland. We established nine transect lines at varying distances from the ice front representing surfaces of age ranging from less than one decade to over 100 years. Each transect consisted of five measurement stations of 1 m^2 where we measured vegetative cover (VC), species richness (SR), and species density (SD) and calculated species evenness (SE). Measurements were made initially in 2007 and repeated at the same geographic coordinates in 2014.

Results: VC increased with distance from the ice front from 16% to over 90%. SR and SD increased from the youngest pioneer community through a mid-successional stage corresponding to an age of over 60 but less than 100 years. Increased VC but declining SR, SD, and SE characterized the oldest (over 100 years) bryophyte-dominated surfaces. Species turnover, which involved forbs almost exclusively, increased moderately from early through mid-successional sites and declined on older sites. Comparison of the measurements made in 2014 to those made in 2007 demonstrates increased SR at mid-successional sites while SD remained relatively constant.

Conclusion: At a small scale, colonization is controlled by local factors such as microtopography and aspect, particularly in proximity to the glacier. At the landscape level, changes in VC and community structure are controlled by time and nutrient availability. Low nutrient levels and limited site availability favor bryophyte dominance on the oldest surfaces. The greatest community-level changes observed over the 7-year interval were increases in surface cover by mosses and low shrubs, particularly in mid-successional and older sites. These changes suggest that the community on the oldest surfaces has not yet reached equilibrium.

Keywords: Primary succession, Glacial foreland, Species richness, Species density, Bryophyte

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Introduction

Forelands exposed by the retreat of glaciers following the conclusion of the Little Ice Age have long been considered optimal settings for the study of rates and processes of landscape modification through floral colonization and pedogenesis (see review in Matthews 1992). Of particular interest is the assessment of the relative importance and interplay of allogenic and autogenic processes in driving species succession as the landscape ages (Matthews and Whittaker 1987; Whittaker 1993). Most of the earlier studies of primary succession, from the late nineteenth and early twentieth centuries, were conducted on the forelands of temperate glaciers in alpine and Scandinavian Europe and North America where the surrounding plant communities are dominated by the boreal forest biome (Coaz 1887; Butters 1914; Cooper 1916, 1931; Lüdi 1921, 1958; Negri 1934, 1936; Fægri 1933; Friedel 1934, 1937, 1938). These glaciers continue to provide useful information for the interpretation of the controls of successional processes on their forelands (Jones and Moral 2005). Particularly well-known are the classic studies that examined the record of 200 years of succession on the glacial foreland in Glacier Bay, Alaska (Crocker and Major 1955; Chapin et al. 1994; Fastie 1995). Of necessity, due mainly to limits of accessibility, few studies have focused on the ecological changes that occur following deglaciation in arctic or subarctic settings, with the major exceptions being those conducted on the forelands of glaciers on Svalbard, which are particularly well studied (Liestøl 1988; Dowdeswell 1995; Liengen and Olsen 1997; Lefauconnier et al. 1999; Liengen 1999; Hodkinson et al. 2003). Notably, Jones and Henry (2003) concluded that the differences in successional processes between temperate and high arctic glacial systems are mainly differences in the species involved and the rates of change, which are faster in temperate environments, not the processes themselves.

The land surfaces exposed in front of many retreating glaciers, whether temperate or high latitude, constitute forelands with a maximum age corresponding to the local maximum advance during the Little Ice Age, and commonly an associated distal outwash plain. The ages of different surfaces within such sequences may be constrained by recessional moraines of known or estimated ages, and therefore these surfaces constitute chronosequences on which rates of various ecological processes can be measured (Vreeken 1975). Nonetheless, measuring primary succession on chronosequences has required a certain level of creativity. The review by Matthews (1992) suggested that one of the most successful approaches is the establishment of permanent plots that can be revisited at multi-year intervals, and the changes recorded. This approach was employed with great success at Glacier Bay, for example (Cooper 1923, 1931, 1939). However, this method may not be practical in some instances, such as in public areas, e.g., national parks.

Recognizing that anthropogenic climate change disproportionately affects higher latitudes (IPCC 2014) has led to renewed interest in landscape-scale ecological and pedogenic processes in arctic and subarctic landscapes, with particular attention to the effects of climate change (Starfield and Chapin 1996; Jägerbrand et al. 2012). Modern climate change has created exceptional opportunities to examine ecological processes and rates of landscape modification in Iceland. Warming is causing the recession of nearly all outlet glaciers of the large Icelandic ice caps, with retreats of well over 1 km documented for many of these glaciers in the last century (Sigurðsson 2005). This recession has exposed fresh surfaces of glacial ice-contact and outwash deposits to floral colonization and soil formation, resulting in the formation of chronosequences with maximum durations of 100 years or more. The study described herein examines the changes in the floral community across the chronosequence of a retreating glacier in southern Iceland with the dual objectives of (1) studying trends in changing floral cover and community structure at various successional stages and attempting to identify the underlying causes, and (2) testing rates of change through comparison of measurements made 7 years apart at the same locations. As a corollary, the study tests the use of Global Positioning System (GPS) data to record the locations of long-term study sites, rather than relying on photographs or maintaining established plots.

Methods

Location and setting

Vatnajökull, the largest ice cap in Iceland (and Europe), measures 7800 km^2 (Baldursson et al. 2018) and is the source of nearly 30 individual outlet glaciers, most of which occupy valleys or broad, subglacial channels (Fig. 1). For the most part, these glaciers reached their Little Ice Age maximum extent near the end of the nineteenth century and have been in a recession much of the time since. Most of these glaciers were in retreat through the 1930s and into the 1940s, responding to a warming climate, but following cooling early in the latter half of the twentieth century, recession rates slowed through the 1950s and 1960s, and some glaciers re-advanced in the late 1960s through 1970s. Consistent warming since the mid-1980s has led to retreat of almost all of these outlet glaciers over the last two decades. Data on the movements of these glaciers have been and continue to be collected by a combination of scientists and local residents. Tabulations of these data are published regularly in the journal *Jökull*. This
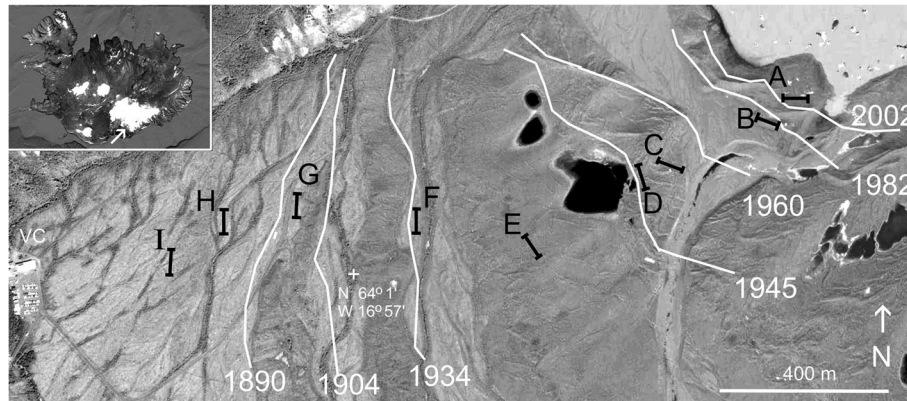
Fig. 1 Map of the sampling sites on the Skaftafellsjökull foreland for 2007 and 2014 with estimated positions of the ice front (see text). Black line segments mark the sample transect locations. Darker areas on the foreland are moraines; lighter areas are terraces of abandoned melt-water streams and bars on the distal outwash plain. These are incised by narrow channels that are darker due to the higher proportion of shrubs and low trees. Inset shows the location of Skaftafellsjökull outlet glacier on southern margin of the Vatnajökull. VC = park visitor center. Figure adapted from imagery downloaded from Google Earth® (image acquisition date August 10, 2015)

database is maintained by the Hydrologic Service of the National Energy Authority (located in Reykjavik).

The retreat of these glaciers over the past century or more has exposed foreland areas with varying topography. Most of the non-surging glaciers have left recessional moraines that can be dated reasonably accurately. For example, at Skaftafell, in Vatnajökull National Park (formerly Skaftafell National Park), the most distal moraine of the Skaftafellsjökull that is clearly identifiable is dated to the position of the ice front from 1890 to 1904. A much more pronounced topography is formed by a set of nested moraines that date from the position of the glacial front in 1945 (Fig. 1). The more proximal moraines date to the positions of the glacial front in 1954, 1960, 1982, and 2002 (Perrson 1964; Sigurðsson 2005; Hannesdóttir et al. 2014). Between the moraines are flat areas formed by alluvial outwash terraces and incised channels. The ages of these inter-moraine surfaces generally are not as well constrained, other than by the moraines that form their boundaries, due to the likelihood of continued reactivation of the outwash channels over the course of many years. Consequently, the surfaces at Skaftafell can best be characterized as pre-1890, 1890–1904, 1904–1945, 1945–1960, 1960–1982, 1982–2002, and post-2002. Nonetheless, the foreland of the Skaftafellsjökull forms a chronosequence, more specifically a post-incisive chronosequence (Vreeken 1975; Huggett 1998) in which distance from the ice front equates (very approximately) to the time of exposure of the surface. The topography of other glacial forelands of the non-surging Vatnajökull outlet glaciers is similar, with prominent moraines formed approximately contemporaneously as those at Skaftafell.

The study site is located at latitude N 64°1.0′ and has a mean elevation of ca. 100 m asl. The southeastern

coast of Iceland is subject to a cool maritime climate. Mean annual precipitation on this area of the south coast is approximately 1800 mm (Vilmundardóttir et al. 2014). The annual mean temperature is 4 °C to 6 °C, with a winter (January) mean of near 0 °C, and a summer (July) mean of 10 °C, although air temperatures in the proximity of the glacier are greatly variable and often significantly cooler. In proximity to the Skaftafellsjökull ice front, the air temperature close to ground level (at 5 cm) has been found to decrease by as much as 9 °C compared to distal locations (Lindröth 1965). The land surface closest to the glacier is also subject to glacial winds of variable strength. Such winds are a common phenomenon formed by the high-temperature gradient immediately above the glacial ice (Hoinker 1954; Geiger 1971). No data specific to the Skaftafellsjökull are available, but the wind has been studied on the outwash plain of the nearby Skeiðarárjökull (Wójcik 1973), where the strength and the effective distance of the wind varies diurnally with solar heating and nightly cooling of the land surface in front of the glacier. Prior to 1967, the study area was farmland (for sheep farming). This area was largely abandoned for grazing after the national park was established in 1967, and formally fenced off in 1987 (Vilmundardóttir et al. 2015a).

Previous work

A survey of species richness at various distances from the glacial ice front was conducted over 50 years ago (Perrson 1964), although the utility of the results is compromised by the locations of the sampling sites. The author intentionally avoided sampling in the topographic low areas (e.g., abandoned melt-water stream channels) and admitted that many of the sample locations were subjected to a microclimate bias from the shelter

afforded by proximity to the rock cliff that borders the glacial foreland (and the glacier) to the west. More recent studies have compared soil composition (carbon and nitrogen content) and vegetative cover at different distances from the ice front (Tanner et al. 2013; Vilmundardóttir et al. 2015a) and the ecology of the soil organisms and their relationship to primary successional processes (van Leeuwen et al. 2018).

Techniques

Nine sites for measurement were selected from a larger set of sites on the Skaftafellsjökull foreland where soil properties were studied previously (Tanner et al. 2013). The sites were chosen to represent locations at varying distances from the ice front, as a proxy for age, and to examine differences in local topography (e.g., five sites on moraines, one site in a channel swale, and three sites on the outwash plain). Site A is the most proximal to the ice front, located on the glacial-facing slope (equals proximal aspect) of the most recent moraine, which is dated to the position of the ice front in 2002 (Hannesdóttir et al. 2014). Site B, located ca. 70 m southwest of site A, is on a flat at the top of the next most proximal moraine from the ice front, associated with the ice position in 1982. Site C is located on the northeast-facing slope (proximal aspect) of a moraine ridge that marks the position of the ice front ca. 1954 (Perrson 1964). Site D is situated in a slight hollow on the southwest-facing slope (away from the glacier or distal aspect) of the moraine ridge from 1954, overlooking a kettle pond in the 1945 moraine. Site E is on a broad flat at the top of the 1945 moraine; the date of deglaciation of the site is estimated at 1938 (based on data from Sigurðsson 2005). Site F is located on the terrace of a stream channel in a swale immediately east (toward the glacier) of the moraine associated with the ice position in 1934 (Sigurðsson 2005). However, this swale was occupied by an outwash channel active as recently as 1960 (Perrson 1964). Site G is situated adjacent to the margin of the oldest boulder moraine, associated with the position of the ice margin between 1904 and 1890. Sites H and I are located on the outwash plain distal (west) of the 1890 ice front. The topography here is not entirely flat but consists instead of very subdued ridges and swales that are relicts of the period when the outwash channels on the plain were occupied. The site I is ca. 140 m south-southwest of site H in a more distal position on the outwash plain (Fig. 1).

At each site, a transect line was established parallel to the ice front with five measurement stations set 10 m apart. Starting points for stations were chosen without bias for substrate, i.e., individual stations may have included non-vegetated boulders. At each station, measurements were made using a 0.5 m × 0.5 m quadrat that

was rotated spatially to provide $1.0\,m^2$ of continuous coverage per station. Within the quadrat, all individual vascular plant species were identified using Kristinsson (2013) as a reference and the percentage of ground area covered by vascular plant species and bryophytes estimated, with each estimate rounded up to the nearest whole percent for the quadrat. Lichens (crustose or other) and biological soil crusts were not included in the species counts. The initial measurements were conducted in early June of 2007; the second set of measurements was conducted in 2014, also in early June, at the coordinates recorded for the sites in 2007. However, it is noted that the accuracy of the GPS instruments used (in 2007 and 2014) allows for meter-scale variation in site location.

Over 50 vascular plants were identified to the species level on the foreland of the Skaftafellsj kull (Table 1). Mosses were not identified to the species level, but substantial portions of the foreland community are dominated by *Racomitrium* spp., particularly *Racomitrium canescens* (hoary fringe moss; Perrson 1964). Similarly, graminoids, other than *Festuca rubra* (red fescue) and *Poa alpina* (alpine meadow grass) were not identified to the species level. The majority of species, particularly among forbs, have very low frequencies of occurrence, typically accounting for less than 1% of cover (but rounded to 1% for all calculations). Commonly, quadrats included one or more specimens with insufficient blossom or leaf characteristics for identification. These individuals therefore are not included in species counts, but their presence is included in estimates of vegetation coverage.

Community structure is represented by assigning all species to the following groups. All bryophytes are grouped as mosses, although as noted above *R. canescens* is dominant. All non-graminoid herbaceous species are designated as forbs. *Empetrum nigrum* (crowberry) is generally the most abundant member of the group designated low shrubs, but other common representatives of the group are *Arctostaphylos uva-ursi* (bearberry), saxifrages, primarily *Saxifraga oppositifolia* (purple saxifrage), *Thymus praecox* (wild thyme), and *Calluna vulgaris* (Scotch heather). The willows and birches have thicker, woodier stems than the other shrubs and therefore are treated as separate groups. The willows consist of the species *Salix lanata* (wooly willow), *S. herbacea* (dwarf willow), and *S. phylicifolia* (tea-leaved willow). Graminoids includes all grasses, fescues, and rushes, of which *F. rubra* and *P. alpina* are the most common. The tree species *Betula nana* (dwarf birch) and *B. pubescens* (downy birch) constitute the final group.

Statistical analyses

For both data series (2007 and 2014), the individual results for each of the four quadrants at each station were

Table 1 List of species identified at Skaftafell in this study (Kristinsson 2013)

Species name	Common name
Alchemilla alpina	Alpine lady's mantle
Arabidopsis petraea	Northern rock cress
Arctostaphylos uva-ursi	Bearberry
Arenaria norvegica	Arctic sandwort
Armeria maritima	Thrift
Bartsia alpina	Alpine bartsia
Betula nana	Dwarf birch
B. pubescens	Downy birch
Bistorta vivipara	Alpine bistort
Botrychium lunaria	Common moonwort
Calluna vulgaris	Scotch heather
Cerastium alpinum	Alpine mouse ear
C. fontanum	Common mouse ear
Draba norvegica	Rock whitlow grass
Dryas octopetala	Mountain avens
Empetrum nigrum	Crowberry
Epilobium anagallidifolium	Alpine willowherb
Equisetum arvense	Field horsetail
E. pratense	Meadow horsetail
Erigeron borealis	Alpine fleabane
Festuca rubra	Red fescue
F. richardsonii	Arctic fescue
Galium verum	Lady's bedstraw
G. normanii	Slender bedstraw
Juniperus communis	Common juniper
Myosotis arvensis	Field forget-me-not
Omalotheca supina	Alpine arctic cudweed
Poa alpina	Alpine meadow grass
Minuartia rubella	Mountain sandwort
Racomitrium canescens (etc.)	Hoary fringe moss (and other mosses)
Rhodiola rosea	Roseroot
Pinguicula vulgaris	Common butterwort
Potentilla crantzii	Alpine cinquefoil
Sagina saginoides	Alpine pearlwort
Salix arctica	Arctic willow
S. phylicifolia	Tea-leaved willow
S. herbacea	Dwarf willow
S. lanata	Wooly willow
Saxifraga oppositifolia	Purple saxifrage
S. cespitosa	Tufted saxifrage
Sedum villosium	Hairy stonecrop
S. acre	Common stonecrop
Selaginella selaginoides	Lesser clubmoss

Table 1 List of species identified at Skaftafell in this study (Kristinsson 2013) *(Continued)*

Species name	Common name
Silene acaulis	Moss campion
S. uniflora	Sea campion
Thymus praecox	Wild thyme
Tofieldia pusilla	Scottish asphodel
Trifolium repens	White clover
Vaccinium uliginosum	Bog bilberry
Veronica alpina	Alpine speedwell
V. fruticans	Rock speedwell

averaged. Thus, for each site, the five stations provide a measure of the species richness (SR), the total number of species present on a surface of consistent age, as well as the local (station to station) variability of the community structure, represented by the standard error of the major elements of the community (e.g., mosses and low shrubs). The species density (SD), the number of species per square meter, was calculated as the mean of the five stations for each site. Additionally, species evenness (SE) was calculated from

$$SE = H/lnSR$$

where H is Shannon's diversity index

$$H = -\sum P_i ln P_i$$

where P_i is the proportion of the population constituted by each species (Hill 1973). Absolute species turnover (β_A) as a function of time (from 2007 to 2014) was calculated for each site by adapting the formula commonly used for a turnover as a function of the spatial distribution

$$\beta_A = (S_{2007} - c) + (S_{2014} - c)$$

where S_{2007} and S_{2014} are the total numbers of species recorded in 2007 and 2014, respectively, and c is the number of species common to both sets of measurements (Albert and Reis 2011).

The significance of the changes in the community at each site from 2007 to 2014 was tested by independent t test of the site data from both series, e.g., site A 2007 data were compared to site A 2014 data. These t test comparisons (2007 vs. 2014) examined changes of total vegetation cover, cover by mosses, and cover by low shrubs with results of significance reported for $p < 0.05$.

Results

The compiled data summaries for total vegetative cover (VC) and cover by each of the groups described above for individual sites as measured in 2007 and 2014 are

presented in Table 2 and shown in Fig. 2. Comparisons of the two major vegetation groups (mosses and low shrubs) for each site in 2007 and 2014 are presented in Fig. 3a. Calculations of SR, SD, SE, and β_A for each site for both 2007 and 2014 are presented in Table 3, along with independent t test comparisons of the 2007 vs. 2014 pairs for each site. Site-by-site comparisons of SR and SD for 2007 and 2014 are shown in Fig. 3b.
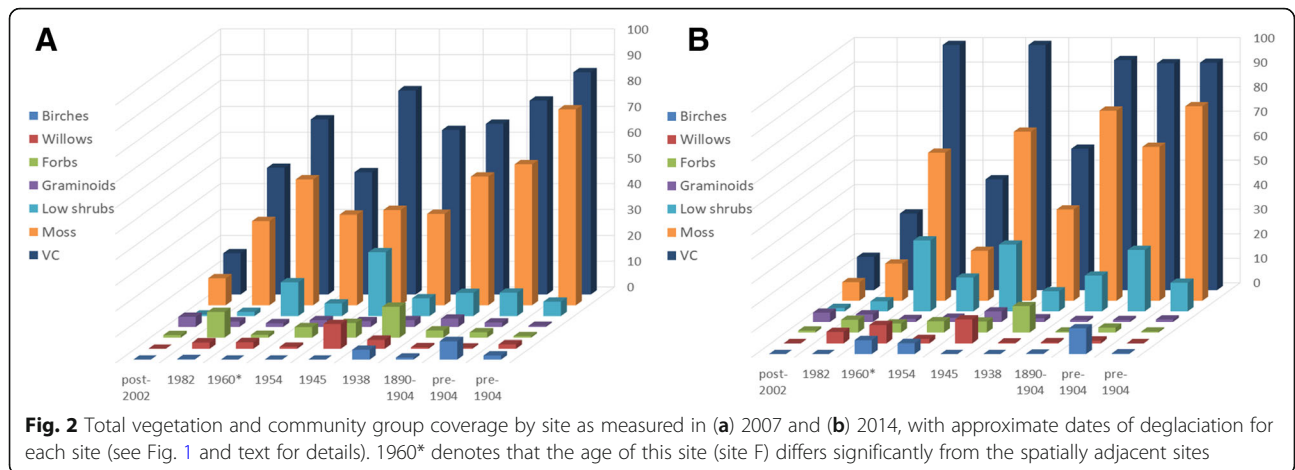
Chronosequence trends

The 2007 and 2014 datasets both demonstrate an overall increase in VC from the sites most proximal to the glacier toward those sites more distal (Fig. 2). The data series for 2007 demonstrates large increases in VC in the early stages of succession, with a major increase between sites A (2002) and B (1982), the former representing a very young surface and the latter corresponding to 35 years of colonization (in 2007). The increase in VC from site A to site B records mainly the increase of mosses, but a substantial increase in forbs also occurred and willows first appeared at this site. SR is near peak value at this site, primarily due to the appearance of seven new species of forbs. Among the low shrubs, *E. nigrum* first appears here. A major increase in VC also occurs between sites C (1954) and D (1945). Although the sites are very close spatially and temporally, they represent very different aspects of the topography. Site C lies on a northeast slope facing the glacier (proximal aspect) and therefore receives less direct sunlight and is

exposed directly to glacial winds; VC and moss have almost the same percentage of coverage as at the much younger site B. Site D, which is on the sheltered southwest-facing slope (distal aspect) demonstrated a substantial increase in VC, primarily through an increase in low shrubs and willows (Fig. 3a). Both SR and SD increased considerably from site C to site D (Fig. 3b). Site E (1938), which is located on a horizontal surface at the top of a moraine (and less sheltered), had lower VC than site D despite the greater age of the land surface; moss coverage remained nearly constant, while forbs increased and the coverage by low shrubs and willows decreased. SR and SD were unchanged from site D to site E. Site F (1960) experienced less exposure time than did site E (1938) but is situated in a more sheltered location. VC was almost the same as at site E, but forbs were much less common and cover by both moss and low shrubs was slightly higher. SR and SD were lower than at site E. The surface at site G (1890–1904), on the margin of the oldest moraine, is approximately 60 years older than site F, but VC and moss coverage were similar to site F, whereas species richness and density both increased. The oldest sites, G, H, and I (the latter two are pre-1904), demonstrated progressive increases in both VC and moss coverage (Fig. 3a), accompanied by progressive decreases in both SR and SD (Fig. 3b).

Overall, the data series for 2014 demonstrates a trend that is broadly similar to that observed in 2007 of increasing VC and moss across the chronosequence,

Table 2 Total vegetative cover (VC), % cover by vegetation groups and site characteristics, 2007 compared to 2014 (with standard error for major groups). See text for explanation of the estimated site age

Class	Sample year	Site A (2002)	Site B (1982)	Site C (1954)	Site D (1945)	Site E (1938)	Site F (1960)	Site G (1890–1904)	Site H (pre-1890)	Site I (pre-1890)
VC	2007	16.0 ± 4.9	49.1 ± 5.9	47.4 ± 8.4	79.1 ± 8.1	63.8 ± 4.5	67.9 ± 8.5	66.2 ± 11.2	75.2 ± 12.1	86.1 ± 9.6
	2014	13.6 ± 2.9	31.2 ± 3.7	45.2 ± 15.7	100 ± 5.6	57.7 ± 11.7	100 ± 8.2	93.8 ± 2.9	92.5 ± 6.9	92.7 ± 11.5
Moss	2007	10.5 ± 5.2	32.7 ± 5.2	35.1 ± 8.5	36.9 ± 3.0	35.4 ± 8.1	48.8 ± 7.4	49.9 ± 13.6	54.7 ± 12.5	76.0 ± 8.8
	2014	7.6 ± 3.4	15.2 ± 3.6	20.4 ± 8.5	69.0 ± 8.2	37.2 ± 13.4	60.4 ± 8.8	77.6 ± 6.3	62.8 ± 16.7	79.4 ± 9.2
Low shrubs	2007	0.6 ± 0.4	1.6 ± 0.9	4.9 ± 1.8	24.8 ± 4.6	6.9 ± 1.4	13.1 ± 5.2	9.0 ± 5.2	9.1 ± 4.4	5.6 ± 2.9
	2014	1.4 ± 0.4	4.1 ± 0.8	13.8 ± 5.1	27.3 ± 7.1	8.2 ± 2.2	29.0 ± 6.1	14.6 ± 5.3	25.1 ± 10.3	11.7 ± 6.7
Graminoids	2007	3.9	2.1	2.6	2.2	2.6	1.4	3.2	1.7	0.4
	2014	3.8	3.1	1.7	4.3	1.5	1.2	0.8	0.8	1.0
Forbs	2007	1.0	10.0	4.1	5.7	12.0	1.1	2.8	2.1	0.6
	2014	0.8	5.2	4.6	4.5	10.8	3.7	0.4	2.0	0.4
Willow	2007	0	2.4	0.8	9.5	3.4	2.5	0.6	0.5	1.7
	2014	0	4.6	1.7	9.7	0.3	7.4	0.4	1.1	0
Birch	2007	0	0.2	0	0	3.8	0	0.8	7.1	1.6
	2014	0	0	4.4	0	0	5.6	0.2	1.4	0.3
Soil N (%)	2007	0.03	0.03	0.16	0.17	0.09	0.18	0.17	0.12	0.14
Surface type		Moraine	Moraine	Moraine	Moraine	Moraine	Channel swale	Moraine margin	Outwash plain	Outwash plain

Fig. 2 Total vegetation and community group coverage by site as measured in (**a**) 2007 and (**b**) 2014, with approximate dates of deglaciation for each site (see Fig. 1 and text for details). 1960* denotes that the age of this site (site F) differs significantly from the spatially adjacent sites

particularly among sites A through D (2002 to 1945). As recorded by the earlier series, site D exhibited a pronounced peak in VC and low shrub cover, although the 2014 set demonstrated a much larger increase in moss cover than seen in 2007. In both data series, site E (1938) has lower VC than site D reflecting a drop in the cover by low shrubs, accompanied by a decrease in moss cover in the 2014 measurement. Unlike the 2007 series, the 2014 series reached peak VC at site F (1960) and maintained consistently high VC and moss and shrub cover through site I (pre-1904; Fig. 3a). SR and SD trends also are similar in both data series, with SR and SD reaching peaks at site E and declining through the remaining sites (Fig. 3b).

Discussion
Changes in community structure
Studies of temperate and Arctic glacier forelands have led to the broad conclusion that succession is a complex process that is difficult to characterize, particularly in the pioneering stage, due to highly variable microsite factors, such as grain size of the substrate and moisture availability, but regardless, it proceeds generally to reach a uniform climax community (Jones and Henry 2003; Burga et al. 2010). This may be the case on the Skaftafellsjökull foreland where succession proceeded from a mixed low shrub-moss heath with abundant forbs in earlier stages to an increasingly moss-dominated heath in later stages (Figs. 2 and 3a). Similar observations were made by Vilmundardóttir et al. (2015b) on the foreland of the Breiðamerkurjökull, another outlet glacier of the Vatnajökull ca. 35 km to the east. At Skaftafell, SR, SD, and species turnover (β_A) increased in the earlier stages and peaked at middle stages, but declined in later stages, as did the coverage by the low shrub assemblage and forbs (Figs. 3a and b). The early stage increases in SR and SD are commonly attributed to facilitation, such as substrate stabilization by the early colonizers (Eichel 2019). The late-stage decline of shrubs and forbs coincided with the increasing domination of the community
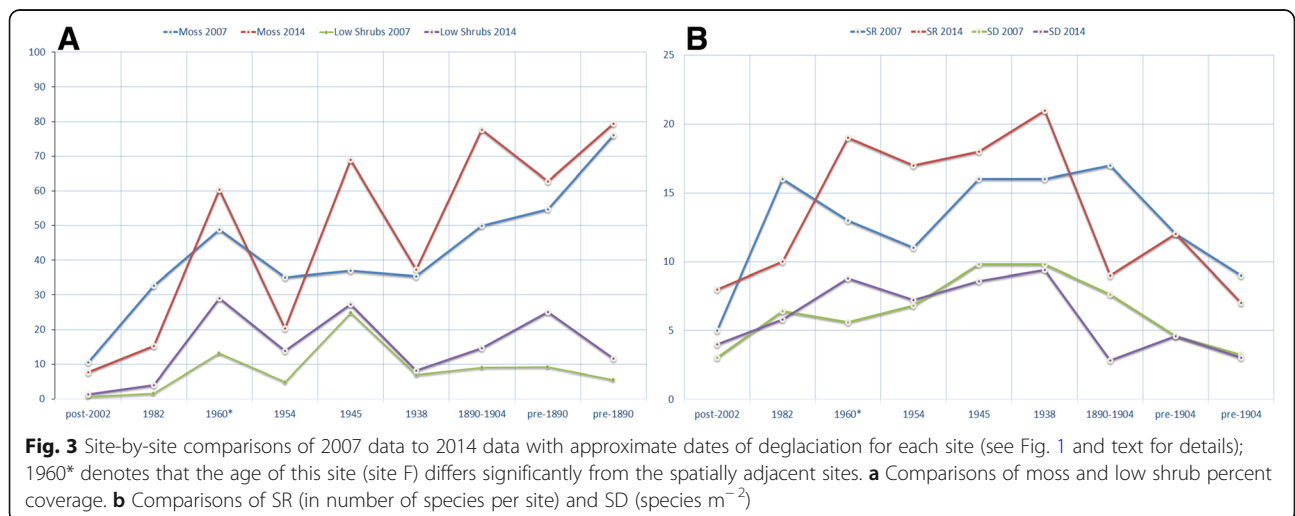

Fig. 3 Site-by-site comparisons of 2007 data to 2014 data with approximate dates of deglaciation for each site (see Fig. 1 and text for details); 1960* denotes that the age of this site (site F) differs significantly from the spatially adjacent sites. **a** Comparisons of moss and low shrub percent coverage. **b** Comparisons of SR (in number of species per site) and SD (species m^{-2})

Table 3 Statistical analyses of species data

Items	Sample year	Site A (2002)	Site B (1982)	Site C (1954)	Site D (1945)	Site E (1938)	Site F (1960)	Site G (1890–1904)	Site H (pre-1890)	Site I (pre-1890)
SR	2007	5	13	11	16	16	16	17	12	9
	2014	8	19	17	18	10	21	9	12	7
SD	2007	3	5.6	6.8	9.8	6.4	9.8	7.6	4.6	3.2
	2014	4	8.8	7.2	8.6	5.8	9.4	2.8	4.6	3.0
SE	2007	0.65	0.42	0.43	0.60	0.43	0.63	0.36	0.40	0.22
	2014	0.56	0.51	0.59	0.45	0.68	0.47	0.33	0.48	0.28
β_A	2007/2014	7	11	11	12	12	12	10	7	6
t test	2007/2014									
VC		ns	0.03	ns	ns	ns	0.026	0.04	ns	ns
Moss		ns	0.024	ns	0.006	ns	ns	ns	ns	ns
Low shrubs		ns	ns	ns	ns	ns	ns	ns	ns	ns

SR species richness (vascular plants), *SD* species density (species/m^2), *SE* species evenness, *VC* vegetative cover, β_A = absolute species turnover, ns (not significant) indicates $p > 0.05$

by mosses, recorded also by decreasing SE (Fig. 3a). The earlier study of the Skaftafellsjökull foreland by Perrson (1964) yielded similar results, although the maximum values for SR and SD reported in that study were higher than we observed. We note, however, that the sampling sites of that study were concentrated mainly within 100 m of the base of the ridge (Skaftafellsheiði) that borders the foreland to the northwest (Fig. 1). The presence of this ridge provides substantial shelter to the northwestern margin of the foreland, which is a birch woodland that may have acted in part as a refugium during the Little Ice Age glacial advance (Lindröth 1965). Nevertheless, the pattern reported herein of SR increasing through the middle stages on the chronosequence and decreasing on the older landscape matches the earlier report (Perrson 1964).

Some studies of glacial forelands have suggested that the early to middle stage peak in SR and SD may reflect the abundance of sites available for colonization, as well as the overlap of species from pioneering and intermediate stages (Jones and Henry 2003). The mid-stage peak and late-stage decline in diversity recorded here by SR, SD, and SE is a trend that has been cited in many studies across successional environments ranging from the Arctic to the tropics (Perrson 1964; Matthews 1992; Zollitsch 1969; Elven and Ryvarden 1975; Connell and Slatyer 1977). Jones and Moral (2005) noted, however, that these results can depend on whether the scale of observation is very local or at the landscape level. Some of these studies have suggested that species competition increases in later stages of succession only when VC approaches near maximum coverage of the foreland (Elven and Ryvarden 1975; Connell and Slatyer 1977; Jones and Henry 2003). Kjær et al. (2018) concluded specifically that species competition in later stages reflects the

relative decrease in abiotic stress that dominates the early successional processes in proglacial environments. The observations presented herein are consistent with the conclusion that competition between bryophytes and vascular species (i.e., forbs and low shrubs) increased as VC increased on surfaces that are both older and at a greater distance from the ice front.

Short-term trends

Precise comparison of data from 2007 to 2014 is somewhat problematic due to the level of small-scale (meter-scale) variation of VC at individual sites, demonstrated by the high standard error associated with many of the measurements, compounded by the meter-scale imprecision of the GPS coordinates. Hence, the few statistically significant differences in the measures at individual sites from 2007 compared to 2014 cannot be attributed unambiguously to successional changes across the 7-year measurement interval. In particular, we note that the measurements at site B recorded a statistically significant decrease in both VC and moss from 2007 to 2014, contrary to the trend of nearly constant (within the range of error) or increasing coverage between the measurements. Otherwise, differences between the two data series are notably consistent and suggest a temporal trend observable at short time scales. Moreover, these results indicate that reliance on GPS coordinates to establish repeated sampling sites, although not ideal and subject to large standard error, is a useful proxy for more permanent site markers.

At sites D (1945) through I (pre-1904), almost all measures indicate higher levels of VC, moss cover, and cover by low shrubs in 2014 than in 2007 (Fig. 3a), with concomitant lower levels of forbs and graminoids. Some of the differences involve species observed at more

proximal sites in 2014 than in 2007. For example, in 2007, the most proximal site where *Epilobium anagalli-difolium* (alpine willowherb) was observed was site B (1982), but in 2014, it was found at site A (2002). Similarly, the most proximal location of *A. uva-ursi* in 2007 was site D (1945), while in 2014, it was recorded at site C (1954). Although not all differences are statistically significant, the consistency of the changes from 2007 to 2014 indicates that the 7-year measurement interval was sufficient to allow measurable successional changes in VC, SR, and community structure.

Notably, at the oldest pre-1890 sites (H and I), the proportion of mosses increased only slightly from 2007 to 2014 whereas low shrub coverage more than doubled. These changes suggest that community structure has not yet reached an equilibrium state on the oldest surfaces. The most distal portion of the Skaftafellsjökull foreland is the outwash plain formed following the Little Ice Age maximum advance, approximately 120 to 130 years ago, but even so, successional processes may not have had sufficient time to achieve a climax community; this may take the form of a mixed low shrub-moss heath that ultimately may be invaded by the birch woodland encroaching from the base of the Skaftafellsheiði ridge to the northwest. The time frame required for successional landscape maturity varies widely and depends very much on local factors (Matthews 1992). On the Storbreen Glacier foreland (southern Norway), for example, measurable successional changes were still occurring on the oldest portions of after 220 years (Matthews 1978).

Importance of aspect

Sites A (2002) and C (1954) are on slopes facing the glacier (proximal aspect) and therefore exposed to the glacial winds, whereas site B (1982) is neutral and site D (1945) faces away from the glacial front (distal aspect) and therefore is sheltered. We suggest that eolian processes associated with the glacial winds provide an inhibitory effect on plant colonization. Periodically these winds may exert an erosive force that may hinder bryophyte colonization due to their lack of anchoring root systems. Additionally, colonization by rooted vascular plants could be reduced if the winds remove or prevent the accumulation of silt-sized substrate between larger gravel and boulders that would otherwise facilitate root penetration and water retention. This role of aspect should decrease with distance, as the strength of the glacial wind decreases with distance from the glacier. This supposition is supported by the relatively small differences in VC between site F (1960), which is much more distal than site C, but is sheltered by its location in a swale between morainal ridges, and the nearby site G (1890–1904), which is not.

Role of facilitation

The significance of nutrient availability as a major control on colonization and succession on glacial forelands has long been a specific research focus. One of the earlier studies of a high-latitude successional setting examined nitrogen fixation resulting from lichen colonization of glacial drift in southern Iceland (Crittendon 1975). Subsequent studies on various glacial forelands on Svalbard focused largely on the contribution of cyanobacterial colonization during the pioneer stage in raising nutrient status prior to vascular plant colonization (Liengen and Olsen 1997; Liengen 1999; Hodkinson et al. 2003; Zielke et al. 2005). Previous investigations of the Skaftafellsjökull foreland found that the nitrogen content in the top 10 cm of soils ranged from < 0.1% at sites more proximal to the ice front to values mainly in the range of 0.1% to 0.2% (maximum 0.26%) at the more distal sites (Tanner et al. 2013; Vilmundardóttir et al. 2015a). Therefore, advanced successional stages did not correlate greatly with soil nitrogen availability, similar to the findings of Robbins and Matthews (2014). Thus, facilitation by nutrient addition appears to be of very limited importance on the Skaftafellsjökull foreland.

The older portions of the foreland are an outwash plain with a subdued ridge and swale topography. The substrate of the ridges consists of coarse glacial outwash deposits that limit the available sites for deep-rooted vascular plants, while the swales contain a higher proportion of finer-grained sediments and host most of the birch trees. Vegetation coverage increased on older surfaces (> 100 years) primarily by the increase of bryophytes due to their lower requirements for nutrients and soil for rooting. Mori et al. (2017) concluded that although SR is strongly influenced by soil properties in early successional stages, the opposite relationship holds in later stages. However, we find no evidence for significant substrate modification at the older sites at Skaftafell, although we concede effective change could occur given much more time, e.g., the bryophytes can act as wind baffles, trapping silt-sized sediments. From our observations, we conclude that the spread of mosses effectively decreased the availability of sites for larger, rooted vascular plants, except in swales that capture the finer-grained sediments that host shrubs and trees. We note, however, that as described above the measurements made in 2014 indicate that the proportion of low shrubs is increasing on the oldest surfaces irrespective of topography.

Notably, to preserve the native community of the landscape, the personnel of the national park has actively prevented the incursion of Arctic Lupine (*Lupinus nootkatensis*), an aggressive invasive species that is common on the south coast of Iceland. Arctic Lupine is a legume and a prolific seed producer that was imported to

Iceland in the early to mid-twentieth century to control soil erosion and reclaim eroded lands because it grows well in nutrient-poor soils and spreads rapidly (Magnússon 2010). The growth of lupine, extensive patches of which occur nearby on the Svinafellsj kull foreland, would promote fixed nitrogen availability in the soil and enhance the growth of vascular plant species, but because it grows quickly and in dense thickets, it displaces other species.

Finally, modern climate warming, which is driving accelerated glacial retreat, might logically be expected to promote more rapid successional changes (Starfield and Chapin 1996). Although the 7-year measurement interval of this study is insufficient to address this question, Hodkinson et al. (2003) concluded that rates of successional change appear to be limited more by nutrient availability. This is not to say that climate change will not affect the composition of the climax community, however. For example, Jägerbrand et al. (2012) found that bryophyte and shrub coverage correlated negatively under natural conditions, but this negative correlation disappeared under artificial warming conditions. Therefore, both autogenic and allogenic processes may play roles in the longer term in controlling both rates and directions of succession (Matthews and Whittaker 1987; Matthews 1992; Whittaker 1993).

Conclusions

Measurements of VC and species counts conducted in 2007 and repeated at the same GPS coordinates in 2014 record a trend of land surface cover increasing from the youngest sites to the oldest on the chronosequence of the Skaftafellsj kull foreland. Both SR and SD increased from the youngest sites through mid-successional stage sites (site E; ca. 1938), but SR, SD, and SE decreased on the oldest portions of the chronosequence, reflecting changes in community structure. Cover by low shrubs, graminoids, forbs, and willows all increased through mid-successional stages but decreased in late stages as mosses became more dominant. We attribute the dominance of bryophytes on older land surfaces to species competition for limited sites on a nutrient-limited landscape.

The results of the study indicate that reliance on GPS coordinates to return to previously measured sites is a useful technique, although imperfect, particularly on younger surfaces where meter-scale variation in vegetation cover is greater. During the 7-year interval between the measurements, VC, cover by mosses and cover by low shrubs all increased at middle to late stages, although most of these changes were not statistically significant. Changes in community structure in 7 years at the late-stage sites, specifically, the increase in the proportion of low shrubs, suggests that succession has not

yet achieved an equilibrium climax community after ca. 100 years. Thus, the oldest portion of the chronosequence may yet transition to a mixed moss-low shrub heath community, or ultimately, to a birch woodland.

Abbreviations
SD: Species richness; SE: Species evenness; SR: Species richness; VC: Vegetative cover

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